

A taxonomic revision of *Oestophora barbula* (Rossmässler, 1838) and *O. barbella* (Servain, 1880), two Iberian endemic land-snail species (Gastropoda: Trissexodontidae)

Revisión taxonómica de *Oestophora barbula* (Rossmässler, 1838) y *O. barbella* (Servain, 1880), dos especies de caracoles terrestres endémicas de la península ibérica (Gastropoda: Trissexodontidae)

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ABSTRACT

Oestophora barbula and *O. barbella* are distinct biological species that can be reliably distinguished only by the longer and stouter penial epiphallus of the former taxon. *Oestophora barbula* is endemic in western-central Portugal, whereas *O. barbella* has a much larger range in western Iberia, including parts of the area occupied by *O. barbula*. Most populations of *O. barbula* have strongly keeled shells and they live mainly in habitats with exposed (Mesozoic) limestone rock. *Oestophora barbella* has the shell periphery rounded to moderately keeled, a small minority of its shells being indistinguishable from some of *O. barbula*. *Oestophora barbella* is found in varied habitats disturbed by man and in more natural situations, some of which have very acidic or strongly basic rocks. It occurs in rocky (Mesozoic) limestone habitats in the Algarve and Serra da Arrábida, but is usually replaced by *O. barbula* in similar habitats over much of western-central Portugal. The two species have been found living together only at one locality in the Serra da Arrábida, where they differ widely in shell size. Type material of both species has been located and lectotypes are designated here.

RESUMEN

Oestophora barbula y *O. barbella* son especies biológicas diferentes, que pueden distinguirse sólo por el epifalo más largo y más grueso del primer taxón. *Oestophora barbula* es un endemismo del oeste y centro de Portugal, mientras que *O. barbella* tiene una distribución mucho más extensa en el oeste de la Península Ibérica, incluyendo partes del área ocupada por *O. barbula*. La mayoría de las poblaciones de *O. barbula* tienen conchas con una fuerte quilla y viven en hábitats expuestos de roca caliza (Mesozoico). *Oestophora barbella* tiene la periferia de la concha redondeada o con una quilla moderada, aunque una pequeña minoría de sus conchas fuera indistinguible de algunos *O. barbula*. *Oestophora barbella* se encuentra en distintos hábitats alterados por el hombre y también en otros más naturales, algunos de ellos con rocas muy ácidas o ultrabásicas. Se encuentra en hábitats de roca caliza (Mesozoico) en el Algarve y la Serra da Arrábida, pero suele estar reemplazado por *O. barbula* en este tipo de hábitats en la mayor parte del oeste y centro de Portugal. Las dos especies se han encontrado simpátricas sólo en una localidad de la Serra da Arrábida, en donde difieren ampliamente en el tamaño de la concha. El material tipo de ambas especies ha sido localizado y se designan aquí lectotipos.

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INTRODUCTION

Oestophora barbula is currently regarded as a widespread and often common land snail throughout the western half of the Iberian Peninsula, readily distinguished from other species of the genus by the usual presence of two palatal teeth in the shell mouth (PUENTE, 1996). Although its local populations vary considerably in shell size and development of a peripheral keel, variation in the genital anatomy has been regarded as rather slight and taxonomically unimportant in most of the recent literature. CASTILLEJO, OUTEIRO AND RODRÍGUEZ (1987) reported some differences in the distal genitalia and in development of a shell keel within coexisting populations in the Serra da Estrela of eastern Portugal, leading them to argue that *O. barbula* was coexisting with *O. barbella* at those localities. However, we agree with PUENTE (1996) that the rather small differences in genital anatomy demonstrated in that study can be attributed to individual variation within a single species.

The first detailed description of the genital anatomy of *O. barbula* by Hesse (1931) nevertheless reported different genital anatomy to that described and figured by almost all subsequent authors (cf. ORTIZ DE ZÁRATE LOPEZ, 1962; MANGA, 1983; CASTILLEJO, 1984; CASTILLEJO ET AL., 1987; PUENTE, 1996), with a much longer and thicker penial epiphallus. ORTIZ DE ZÁRATE LÓPEZ (1962) attributed this difference to the epiphallus in Hesse's material being swollen due to the supposed presence of a spermatophore inside, a suggestion later cited by PUENTE (1996). However, this seems unlikely as the shape of the spermatophore in Helicacea is determined by the internal shape of the epiphallus in which it forms, rather than *vice-versa*. Hesse dissected three individuals from near Lisbon and he presented three drawings (HESSE, 1931: Taf. 8, Figs. 63A-C) each showing similar anatomy with a large epiphallus, so it anyway seems unlikely that all three should have the epiphallus similarly distended by a

spermatophore which Hesse did not notice.

The present paper reports a study of *Oestophora barbula sensu lato* from Portugal and neighbouring regions of Spain. It soon became apparent that many populations from western-central Portugal show the large epiphallus figured by Hesse and these were mainly also characterised by strongly keeled shells. Rossmässler's type material of *O. barbula* appears to be of this localised endemic form. All other populations studied resembled Spanish material in having a smaller epiphallus and they almost always lacked a really strong keel on the shell; the oldest valid name applicable to this form is *O. barbella* (Servain, 1880). Lectotypes are designated here for both names. The two taxa live close together in parts of western Portugal and living populations of both with no intermediates were collected from beneath the same boulders at one locality in the Serra da Arrábida. We also discuss variability in shell morphology and problems of species identification from shells, and apparent differences in the range of habitat preferences of each species.

MATERIAL AND METHODS

Field collections by the authors consisted of all mature shells found, to avoid possible bias in favour of large specimens. Localities and altitudes were recorded mainly using a Garmin Etrex High Sensitivity hand-held GPS, accurate to within 10 metres. From 2007 onwards sites were given consecutive serial numbers (e.g. P37). Habitat notes (including bedrock type and vegetation) and associated Mollusca were also recorded at all sites. Adult snails could readily be recognised by the thickened, reflected lip to the shell mouth and these normally had enlarged distal genitalia. Living adult specimens collected by the authors for anatomical study were drowned by immersion in water overnight, transferred to 80% Industrial Methylated Spirit, then pulled or part-

pulled from the shell when the body hardened after a few days. "Proximal" and "distal" refer to the position in relation to the ovotestis. Drawings of the distal genital anatomy were prepared using a Meiji drawing tube on a Meiji RZ series stereomicroscope.

Measurements of shell breadth and height, and counts of whorls followed the methods described by KERNEY AND CAMERON (1979). These shell measurements were made on adult shells to the nearest 0.1 mm using an eye-piece graticule in a stereo-microscope. Accuracy of the counts of whorls was slightly reduced by the protoconch often appearing somewhat triangular when viewed from above, rather than semicircular. Measurements of (greatest) width of umbilicus and the breadth of the same shell were measured using Infinity Analyze© software on images of adult shells taken with an Infinity 1 camera on a Meiji RZ series stereomicroscope. The measurements on the images were reproducible to $\pm < 0.01$ mm, but unavoidable slight tilting of the shells almost certainly caused some additional loss of precision.

Full details of specimens studied by the authors are listed in the Appendix, which includes all those used for anatomical study. In addition notes on shells in the Coimbra, Lisbon and Porto Museums were kindly supplied by Álvaro De Oliveira, along with specimens and data from his personal collection; this information has been added to the distribution maps. Two syntypes of *O. barbula* were studied from high quality photographs supplied by the Forschungsinstitut Senckenberg. 12 syntypes of *O. barbella* were studied on loan from the Bourguignat Collection housed at the Muséum d'Histoire Naturelle, Ville de Genève. The remainder of the material studied is retained in the Collection of G.A. and D.T. Holyoak.

RESULTS AND DISCUSSION

Genital anatomy. The genital anatomy of *O. barbella* from Spain was carefully

and accurately described by PUENTE (1996) under the name *O. barbula* with clear drawings of nine individuals. Hence the present account concentrates on the differences between *O. barbella* and *O. barbula*, which appear to be confined to the distal genitalia, especially the epiphallus and penis (Figs. 1-2).

In the present study, distal genitalia have been dissected and described in detail from 142 individual snails representing 66 populations (listed in Appendix). *O. barbula* was represented by 35 individuals (+ 1 with genitalia too immature to be useful), representing 16 populations; *O. barbella* was represented by 102 individuals (+ 4 with genitalia too immature to be useful), representing 49 populations. Only one population (7 individuals, from site P67/P161) could not be securely assigned to either taxon on the basis of the epiphallus; the identity of this unusual population is discussed below.

Figures 1-2 give representative drawings of the penis and epiphallus in varied individuals of each species. Table I compares measured proportions of epiphallus length relative to penis length and thickness of epiphallus compared to thickness of penis. In mature individuals, the epiphallus length is generally less than half the penis length in *O. barbella*, more than half the penis length in *O. barbula*. The thickness of the epiphallus is generally less than that of most of the penis (the epiphallus appearing thin-walled) in *O. barbella*, equal to or more than that of most of the penis (and appearing muscular and thick-walled) in *O. barbula*. Combining the length and thickness criteria left very few individual snails that were difficult to assign to one species or the other. Study of the internal structures of penis and epiphallus of a few individuals did not reveal any clear interspecific differences.

A single population (P67/P161: ca 2.3 km NE. of São Pedro de Moel, Estremadura) remained problematical with seemingly intermediate epiphallus characteristics based on seven mature specimens (epiphallus relatively long but usually no stouter than penis: Fig. 2G). On the basis of the epiphallus length

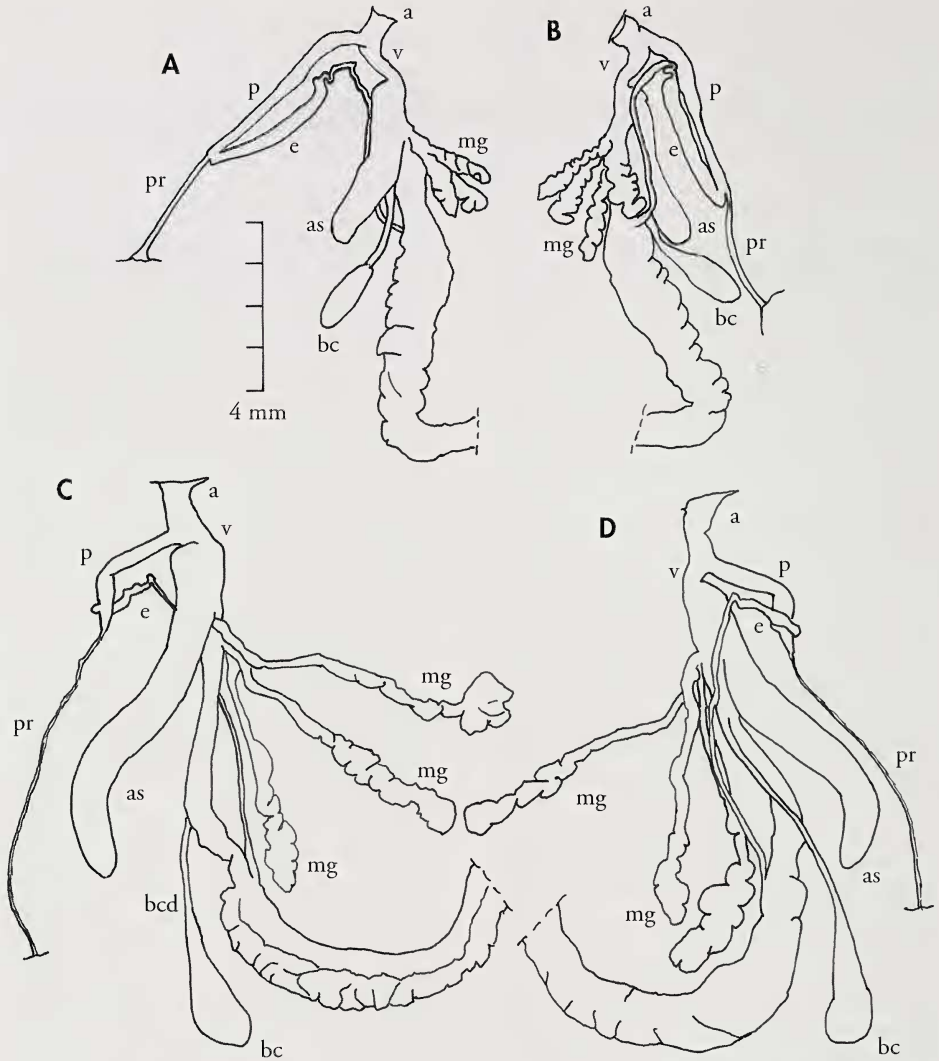


Figure 1. Anatomy of distal genitalia in representative specimens of *Oestophora* from Portugal. A: *O. barbula* (Rossmässler, 1838), 2 May 2010, SE. of Moitas Venda, Ribatejo (slightly atypical specimen with four mucus glands); B: same specimen viewed from opposite side; C: *O. barbella* (Servain, 1880), 3 Nov. 2010, NW. of Verride near Rio Mondego, Beira Litoral; D: same specimen viewed from opposite side (specimens in collection of G.A. and D.T. Holyoak). Abbreviations, a: atrium; as: accessory sac on vagina (with small dart sac at distal end); bc: bursa copulatrix; bcd: bursa copulatrix duct; e: epiphallus; mg: mucus gland; p: penis; pr: penis retractor; v: vagina; vd: vas deferens.

Figura 1. Anatomía de los genitales distales en ejemplares representativos de *Oestophora* de Portugal. A: *O. barbula* (Rossmässler, 1838), 2 may. 2010, SE. de Moitas Venda, Ribatejo (ejemplar un poco atípico, con cuatro glándulas mucosas); B: mismo ejemplar visto desde el lado opuesto; C: *O. barbella* (Servain, 1880), 3 nov. 2010, NW. de Verride cerca de Río Mondego, Beira Litoral; D: mismo ejemplar visto desde el lado opuesto (ejemplares en la colección de G.A. y D.T. Holyoak). Abreviaturas, a: atrio; as: saco accesorio en la vagina (con pequeño saco del dardo en el extremo distal); bc: bursa copulatrix; bcd: conducto de la bursa copulatrix; e: epifalo; mg: glándula mucosa; p: pene; pr: retractor del pene; v: vagina; vd: vaso deferente.

Table I. Relative size of epiphallus and penis in *Oestophora barbula* and *O. barbella*. Data are given only for individuals with distal genitalia sufficiently large to be regarded as mature or close to maturity. N = number of individuals.

Tabla I. Tamaño relativo del epifalo y del pene en *Oestophora barbula* y *O. barbella*. Los datos se dan sólo para los individuos con genitales distales suficientemente grandes como para ser considerados maduros o cerca de la madurez. N = número de individuos.

Epiphallus length/penis length		0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6
<i>O. barbula</i>	N	-	-	-	-	2	2	4	5	14	4	1	1	-	1	1
<i>O. barbella</i>	N	21	58	14	6	2*	1†	-	-	-	-	-	-	-	-	-
P67/161: S. Pedro de Moel	N	-	-	-	1	2	3	-	1	-	-	-	-	-	-	-

* = 1 of these deformed,
 † = with abnormally short penis

Epiphallus thickness: penis thickness		thinner	± equal	thicker
<i>O. barbula</i>	N	-	3	32
<i>O. barbella</i>	N	95	6	1
P67: S. Pedro de Moel	N	-	6	1

they were certainly closer to *O. barbula*, but the small, unkeeled shells (Table II, Figs. 4G-I) were superficially much more similar to those of some *O. barbella*. However, the proportionately very small umbilicus is much more like that of *O. barbula* than of populations of *O. barbella* from western-central Portugal (cf. Table III, Figs. 3, 4 and notes below). Nevertheless, the habitat was more like that of other material confirmed as *O. barbella* (among limestone boulders used to construct the abutment of a small bridge over a stream in a coastal region with unconsolidated Quaternary sands supporting a tall *Eucalyptus* plantation; see below for additional information). The possibility that this population represents an undescribed third species seems unlikely in view of its lack of any unique characters, the single locality and the disturbed habitat. Hence it is tentatively regarded here as a population of *O. barbula* with shells that lack a keel and show a relatively narrow umbilicus, although further study is needed in view of the relatively weak epiphallus and habitat atypical for that species (see below).

The functional explanation of the longer, thicker epiphallus of *O. barbula*

compared to that of *O. barbella* is uncertain. It is noteworthy that the epiphallus is approximately similar in length to the bursa copulatrix duct in *O. barbula* (ratio ca 1:1, Figs. 1A, B), whereas the epiphallus is much shorter and the bursa copulatrix duct much longer in *O. barbella* (ratio ca 1:3, Figs. 1C, D). Hence, it might be surmised that if a spermatophore is formed inside the epiphallus as usual in many (if not all) species of Helicacea, it will be longer in *O. barbula* than in *O. barbella*. Indeed, the epiphallus in *O. barbella* is so short in comparison to its bursa copulatrix duct that a spermatophore formed inside it would apparently be too short for effective fertilisation in the manner described for *Helix pomatia* L. by LIND (1973) and currently assumed to be widespread in Helicacea. This fertilisation mechanism involves the spermatophore lodging inside the bursa copulatrix duct, so that when some of the spermatozoa it contains escape through its tail canal they reach the spermatheca by way of the oviduct. Corresponding to this widely accepted model of the fertilisation process, KOENE AND SCHULENBERG (2005) found correlations between the length of the penial flagellum and the spermatophore-receiving organ in helicoid land

snails in general, indicating coevolution which probably results from counter-adaptation between male and female reproductive organs that may control fertilisation. Likewise, SAUER AND HAUSDORF (2009) demonstrated a positive scaling between male spermatophore producing organs and female spermatophore-receiving organs in *Xerocrassa* species (Hygromiidae *sensu lato*) from Crete, indicating sexual coevolution which they attributed to sexual selection processes. The relative lengths of epiphallus and bursa copulatrix duct in *O. barbula* and *O. barbella* differ so markedly from results of these studies that further study is needed. Spermatophores have apparently not been described in the literature for *Oestophora* and they were not

noticed during the present study. Hence, it should be established whether the spermatozoa are transferred in spermatophores in both species, and whether or not self-fertilisation is common. Mating was seen only once during our fieldwork, a pair of *O. barbella* in coitus being collected on 3 November 2010, at ca 11.00 hours, on the undersurface of a limestone boulder, 1 km NW. of Verride near the Rio Mondego, Beira Litoral.

SEIXAS (1976) gave a confused account of a Portuguese *Oestophora* under the name "*Mastigophalus rangi* (De Férussac, 1839)", concluding that *Oestophora lusitanica* (L. Pfeiffer, 1841) may be the same species as that correctly known as *Mastigophallus rangianus* (Férussac, 1822). The latter is

(Right page) Figure 2. Distal male genitalia in representative specimens of *Oestophora* from Portugal. A-F: *O. barbula* (Rossmässler, 1838), G: *O. cf. barbula* (atypical population with unkeeled shells) and H-N: *O. barbella* (Servain, 1880); drawings show genitalia *in situ*, partly dissected to reveal penis and epiphallus, but with only distal ends of penial retractor muscle and vas deferens drawn. A, B: 9 Jan. 2011, by Paul do Taipal near Montemor-o-Velho, Beira Litoral; C: 13 Jan. 2011, summit area of Serra de Sico, Beira Litoral; D: 12 Feb. 2008, Serro Ventoso, Estremadura; E: 29 Apr. 2011, just NE. of Ansião, Beira Litoral; F: 12 Feb. 2011, Serra da Arrábida, Estremadura, population coexisting with *O. barbula*, cf. Fig. 2L; G: 4 June 2011, 2 km NNE. of S. Pedro de Moel, Estremadura, individual with longest epiphallus and (uniquely) a single minute flagellum; H: 20 Oct. 2008, Cerrinho das Neve, Mértola, Baixo Alentejo, Topotype; I: 15 Jan. 2011, SW. of Proença-a-Velha, Beira Baixa; J: 5 Feb. 2011, W. slope of Foia, Algarve; K: 28 Jan. 2011, by N2 NNW. of Alportel, Algarve; L: 12 Feb. 2011, Serra da Arrábida, Estremadura, population coexisting with *O. barbula*, cf. Fig. 2F; M: 3 May 2011, S. of Costa Nova do Prado, Beira Litoral; N: 27 Oct. 2010, 1 km NW. of Gafanha do Areão, Beira Litoral (all specimens in Collection of G.A. and D.T. Holyoak). Abbreviations as in Figure 1, plus or: ommatophore (with black or grey parts stippled) and its retractor muscle.

(Página derecha) Figura 2. Genitales masculinos distales en ejemplares representativos de *Oestophora* de Portugal. A-F: *O. barbula* (Rossmässler, 1838), G: *O. cf. barbula* (población atípica, con conchas sin quilla) y H-N: *O. barbella* (Servain, 1880); los dibujos muestran los genitales *in situ*, diseccionados en parte para revelar el pene y el epifalo, pero representando sólo los extremos distales de los músculos retractores del pene y del vas deferens. A, B: 9 ene. 2011, junto a Paul do Taipal cerca de Montemor-o-Velho, Beira Litoral; C: 13 ene. 2011, zona de la cumbre de la Serra de Sico, Beira Litoral; D: 12 feb. 2008, Serro Ventoso, Estremadura; E: 29 abr. 2011, inmediatamente al NE. de Ansião, Beira Litoral; F: 12 feb. 2011, Serra da Arrábida, Estremadura, la población conviviendo con *O. barbula*, véase Fig. 2L; G: 4 jun. 2011, dos km. al NNE de S. Pedro de Moel, Estremadura, ejemplar con el mayor epifalo y (singularmente) un solo flagelo diminuto; H: 20 oct. 2008, Cerrinho das Neve, Mértola, Baixo Alentejo, topotipo; I: 15 ene. 2011, SO. de Proença-a-Velha, Beira Baixa; J: 5 feb. 2011, ladera oeste de Foia, Algarve; K: 28 ene. 2011, por la N2, NNO. de Alportel, Algarve; L: 12 feb. 2011, Serra da Arrábida, Estremadura, la población conviviendo con *O. barbula*, véase Fig. 2F; M: 3 may. 2011, S. de Costa Nova do Prado, Beira Litoral; N: 27 oct. 2010, 1 km NO. de Gafanha do Areão, Beira Litoral (todos los ejemplares en la colección de G.A. y D.T. Holyoak). Abreviaturas como en la Figura 1, además de or: ommatóforo (con partes negras o gris punteadas) y su músculo retractor.

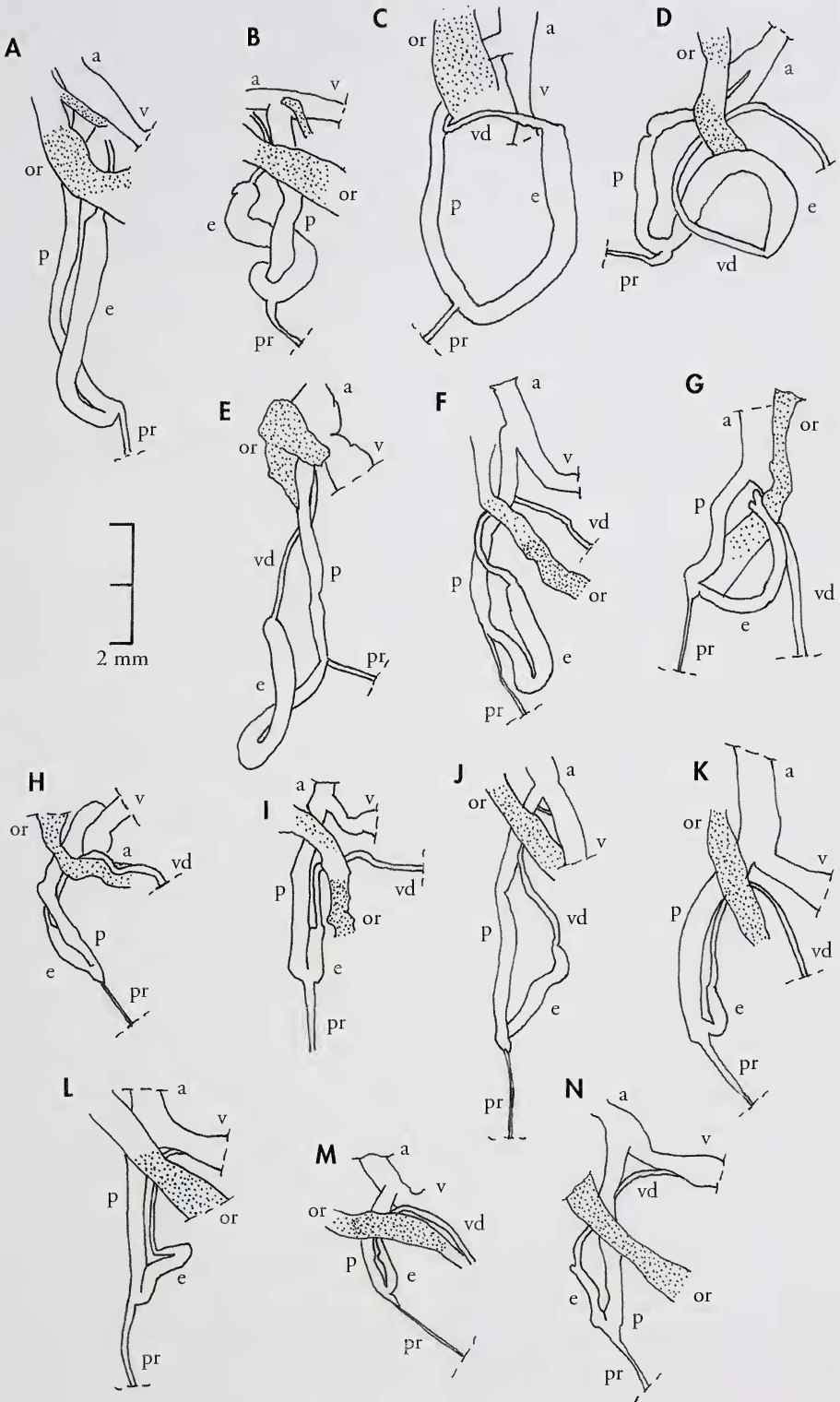


Table II. Measurements of shells of *Oestophora barbula* and *O. barbella*. Data are given only for populations identified anatomically from epiphallus structure by the authors, for which 7 or more adult shells were available (specimens in authors' collection). N= number of individuals; s.d.= sample standard deviation. Rock types at each site are coded as follows, DS: coastal sand dunes; LB: limestone boulders placed to reinforce river banks, and a bridge abutment; Ls: limestone bedrock; Sh: shale; Sl: slate; Ss: sandstone.

Tabla II. Mediciones de conchas de *Oestophora barbula* y *O. barbella*. Los datos se dan sólo para las poblaciones identificadas por los autores a partir de la estructura anatómica del epifalo, de las cuales se disponía de 7 o más conchas de adultos (ejemplares en la colección de los autores). N= número de individuos; s.d.= Desviación estándar de la muestra. Tipos de roca en cada sitio representados como sigue, DS: dunas de arena costeras; LB: rocas calizas formando riberas artificiales o el embasamiento de un puente; Ls: afloramiento de roca caliza; Sh: esquistos; Sl: pizarras; Ss: areniscas.

Site	Locality	Rock	N	Breadth				Height				Whorls			
				max	min	mean	s.d.	max	min	mean	s.d.	max	min	mean	s.d.
<i>O. barbula</i>															
P129	Serra da Arrábida	Ls	22	9.5	7.5	8.51	0.546	4.9	3.5	4.20	0.402	5.7	5.0	5.41	0.229
P130	Serra da Arrábida	Ls	66	10.9	8.8	9.65	0.501	5.2	3.9	4.47	0.254	6.1	5.1	5.48	0.228
P131	Serra da Arrábida	Ls	11	11.0	9.4	10.34	0.607	4.9	3.8	4.49	0.324	5.7	5.0	5.35	0.246
P98	Serra de Sico	Ls	12	12.3	10.6	11.54	0.512	5.9	4.8	5.37	0.317	6.2	5.3	5.83	0.218
P41	SE. of Moitas Venda	Ls	27	13.0	10.5	11.65	0.605	6.0	4.3	4.93	0.376	6.2	5.3	5.74	0.274
P79	SW. of Alfaielos	Ls	12	12.6	10.7	11.68	0.636	5.7	4.5	5.16	0.446	5.8	5.1	5.44	0.215
P59	SW. of Serra Ventoso	Ls	13	12.9	11.4	12.17	0.435	5.7	4.4	5.07	0.343	6.3	5.3	5.89	0.312
P96	near Paul do Taipal	Ls	9	12.7	12.2	12.49	0.162	5.6	5.0	5.42	0.186	5.9	5.7	5.78	0.067
P73d	WNW. of Ansião	Ls	24	13.7	11.6	12.67	0.585	6.4	5.0	5.67	0.399	6.3	5.4	5.92	0.245
<i>O. barbula?</i>															
P67/															
P161	NE. S. Pedro de Moel	LB	23	10.2	8.8	9.43	0.452	5.0	4.1	4.60	0.283	6.2	5.3	5.69	0.299
<i>O. barbella</i>															
P100	SW. Proença-a-Velha	Sl	8	8.8	7.2	7.78	0.526	4.3	3.4	3.74	0.320	5.7	4.3	4.76	0.441
P88	W. of Ladoeiro	Sl	15	9.4	6.8	8.28	0.713	4.8	3.1	3.98	0.487	5.6	4.3	4.99	0.344
P76	NW. Gafanha do Areão	DS	39	10.2	8.2	9.47	0.496	5.5	3.8	4.66	0.334	5.8	4.9	5.50	0.210
P97	S. of São Pedro	DS	14	10.5	8.7	9.55	0.556	5.2	4.2	4.76	0.295	5.9	5.2	5.53	0.205
P128	Serra da Arrábida	Ls	28	10.7	8.5	9.58	0.573	5.3	3.9	4.66	0.313	5.9	5.2	5.52	0.206
P119	Serra de São Miguel	Ls	8	10.6	8.6	9.60	0.697	5.2	4.3	4.66	0.297	5.5	4.8	5.18	0.231
P144	S. of C. N. do Prado	DS	7	11.2	10.1	10.60	0.443	4.7	4.1	4.44	0.215	6.2	5.8	6.07	0.160
P129	Serra da Arrábida	Ls	16	11.6	9.8	10.63	0.440	5.7	4.6	5.05	0.344	5.9	5.5	5.71	0.109
P80	N. of Ameal	LB	15	11.8	9.9	10.81	0.579	5.6	4.5	5.01	0.370	6.2	5.4	5.74	0.229
P110	NW. from Ameixial	Sl, Sh	7	13.3	10.5	11.73	1.126	6.0	4.8	5.37	0.544	6.1	5.2	5.74	0.299
P37	W. edge Sertão	Sl	7	13.5	11.4	12.49	0.851	6.0	5.5	5.81	0.212	6.1	5.5	5.76	0.230
P72	Barcoila, nr Cabeçudo	Sl	7	13.6	11.8	12.51	0.654	6.6	5.7	6.03	0.350	5.9	5.4	5.74	0.181
P106	NNW. of Alportel	Sl, Ss	10	14.2	12.0	13.54	0.631	6.0	5.5	5.80	0.194	5.7	5.2	5.54	0.190

generally regarded as a distinctive endemic species restricted to a small coastal region in S. France (Depts Pyrénées Orientales and Var) and NE. Spain (Prov. Gerona) (PUENTE, ALTONAGA, PRIETO AND RUIZ, 1998: 47). Shells of

these taxa have very little in common, *O. lusitanica* having a rounded shell periphery and no apertural teeth, *M. rangianus* having a sharp keel and prominent apertural teeth. It is unclear whether the Portuguese specimens des-

Table III. Relative width of the umbilicus in shells of *Oestophora barbula*, *O. barbella* and a population of *O. cf. barbula* from near S. Pedro de Moel (Estremadura). The data on *O. barbula* are based on 20 representative mature shells selected from 6 populations; those on *O. barbella* on 22 representative mature shells from 7 populations within western-central Portugal (Coimbra to Serra da Arrábida). N = number of shells.

Tabla III. Anchura relativa del ombligo en conchas de *Oestophora barbula*, *O. barbella* y una población de *O. cf. barbula* de cerca de S. Pedro de Moel (Estremadura). Los datos de *O. barbula* se basan en 20 conchas de individuos maduros seleccionadas en 6 poblaciones, los de *O. barbella* en 22 conchas de individuos maduros de 7 poblaciones en el oeste y centro de Portugal (Coimbra hasta Serra da Arrábida). N = número de conchas.

Width of umbilicus as per cent of shell breadth		12	13	14	15	16	17	18	19	20	21	22	mean
		-13	-14	-15	-16	-17	-18	-19	-20	-21	-22	-23	
<i>O. barbula</i>	N	-	-	-	-	4	5	5	4	1	1	-	18.35%
<i>O. barbella</i>	N	-	-	-	-	-	-	2	9	5	2	4	20.38%
<i>O. cf. barbula</i> samples P67/161 from S. Pedro de Moel	N	1	1	4	2	7	4	1	-	-	-	-	15.98%

cribed by Seixas were *O. lusitanica* or *O. barbula sensu lato*, since the shell description does not mention teeth. Her drawing of the genital anatomy (SEIXAS, 1976: 36, Fig. 8D) is also unclear, with the organ labelled "p." [enis] apparently representing the accessory sac on the vagina and hence no distal male genitalia were shown. In view of these uncertainties the information given by Seixas seems best disregarded.

Shell characters. Shells of *O. barbula* and *O. barbella* have been compared closely using samples identified from epiphallus structure. The most consistent difference is that *O. barbula* has a sharp to very sharp peripheral keel on the body whorl of adult shells, whereas most *O. barbella* have the periphery lacking a keel (slightly angled to bluntly keeled or rounded) (Figs. 3, 4). Only a very small minority of shells of *O. barbella* have a keel sufficiently developed to allow confusion with shells of *O. barbula* (e.g. some shells from Verride, Beira Litoral: Fig. 4O).

CASTILLEJO ET AL. (1987) found that development of a peripheral keel is quite variable within some local populations in the Serra da Estrela (Beira Alta) that we interpret as being composed entirely of *O. barbella*. MATOS (2004: 105) claimed that populations of *O. barbula* [*sensu lato*],

both wild and reared under laboratory conditions, frequently show shells with a more or less strong equatorial keel. The proportion of keeled individuals was said to vary around 20-28% in a single population or in the total population, these values corresponding to typical Mendelian segregation of a recessive gene, according to results then awaiting publication. With *O. barbella* we have not found any clear demarcation between keeled, slightly keeled, slightly angled (commonest type) and rounded shells in most populations, whereas *O. barbula* is consistently keeled. PUENTE (1996: 88) mentioned shells as being clearly rounded in five Spanish populations [of the taxon we regard as *O. barbella*] and clearly angular in one population (from Las Correderas in Prov. Jaén).

The only other shell character likely to be helpful in distinguishing the two species is that most populations of *O. barbula* have a proportionately narrower umbilicus than most populations of *O. barbella*, at least within western-central Portugal (Table III). With careful measurements of adult shells (see above), umbilicus widths of less than 18% of shell breadth were found only in *O. barbula*, whereas those above 20% were found mainly in *O. barbella*. The small difference in umbilicus width is appa-

rently due mainly to the tendency for *O. barbula* to have the body whorl wider in proportion to its height, as reflected in the tendency for the shell mouth to be more elliptical in *O. barbula*, more rounded in *O. barbella*. Most shells from many populations of *O. barbella* show an umbilicus that becomes asymmetrical during growth because of the form of the body whorl, whereas the smaller umbilicus of *O. barbula* is usually more symmetrical. However, individual shells often contradict these generalisations.

Detailed data on shell sizes and number of whorls is presented in Table II, for populations that have been identified from the epiphallus structure and which include >6 adult shells, so that mean sizes, size ranges and standard deviations can be estimated with at least modest reliability. Shell size varies widely from locality to locality in both species, although *O. barbella* has populations with both smaller and larger mean shell breadths than *O. barbula* (Table II).

It is difficult to detect any consistent regional patterns in the distribution of mean shell size for either species, with little hint of any orderly pattern in size or shape that might be used to define geographical subspecies. The most obvious overall trend is apparently towards small shell size in drier local habitats or regions and larger shell size in wetter or more humid situations. This is most obvious in *O. barbella*, where the two samples with smallest shell breadth (P88, P100) are from areas of eastern Beira Baixa with low regional rainfall and hot dry summers, followed by two samples from coastal sand dunes (P76, P97), then three samples from open karst areas on Mesozoic limestone hills (P128 and P129 on Serra da Arrábida, P119 from Serra de São Miguel). The largest shells are from sites on hills of slate and other siliceous rocks, with relatively high rainfall. A review by GOODFRIEND (1986) similarly found that within a land-snail species larger shell size is often associated with moist environments. Smaller size was also sometimes recorded at higher population densities, apparently through effects of pheromones on growth rates, but the latter

tendency was not apparent in these *Oestophora* species. Reduced size of *O. barbula* living sympatrically with *O. barbella* at one of the sites in the Serra da Arrábida might be a consequence of interspecific competition, as discussed below.

The ratio of shell height (H) to shell breadth (B) overlaps very widely in *O. barbula* and *O. barbella*, population means being within an overall range of $H = 0.42-0.49 B$ in the former species, $0.42-0.50 B$ in the latter species. The number of shell whorls tends to be slightly higher in *O. barbula* (overall range 5.0-6.3, population means 5.35-5.92) than in *O. barbella* (overall range 4.3-6.2, population means 4.76-5.76) (Table II), but there is much overlap and a strong tendency within populations of both species for smaller shells to be comprised of fewer whorls. Development of the palatal teeth is rather variable, with the inner tooth being absent in a small percentage of *O. barbella*, but apparently always being present in mature *O. barbula*.

Although shells of both species seem at first sight to have rather variable surface sculpture, close study at high magnification (up to $\times 40$) with a stereomicroscope suggests that both have a very similar basic pattern that does not allow species identification. The surface of the protoconch is virtually smooth, the same lack of sculpture continuing on whorl 0-0.3. Whorl 0.3-0.7 has irregular low radial ribs, formed by elongate papillae. Whorls 0.7-1.4 have about 8-12 raised ridges, which show some tendency to spiral around the shell whorl but soon descend into the lower suture; around whorls 1.4-1.6 these ridges are reduced to spiral lines of low scales. After whorl 1.6 the sculpture of the mature teleoconch develops, with increasingly prominent, long, low radial ribs, with small raised papillae on a rectilinear grid in the valleys between the ribs. Much of the apparent variability in sculpture on samples of mature shells results from differences in the strength (height) of ribs on later whorls of the teleoconch and the extent to which these are developed on the underside of the

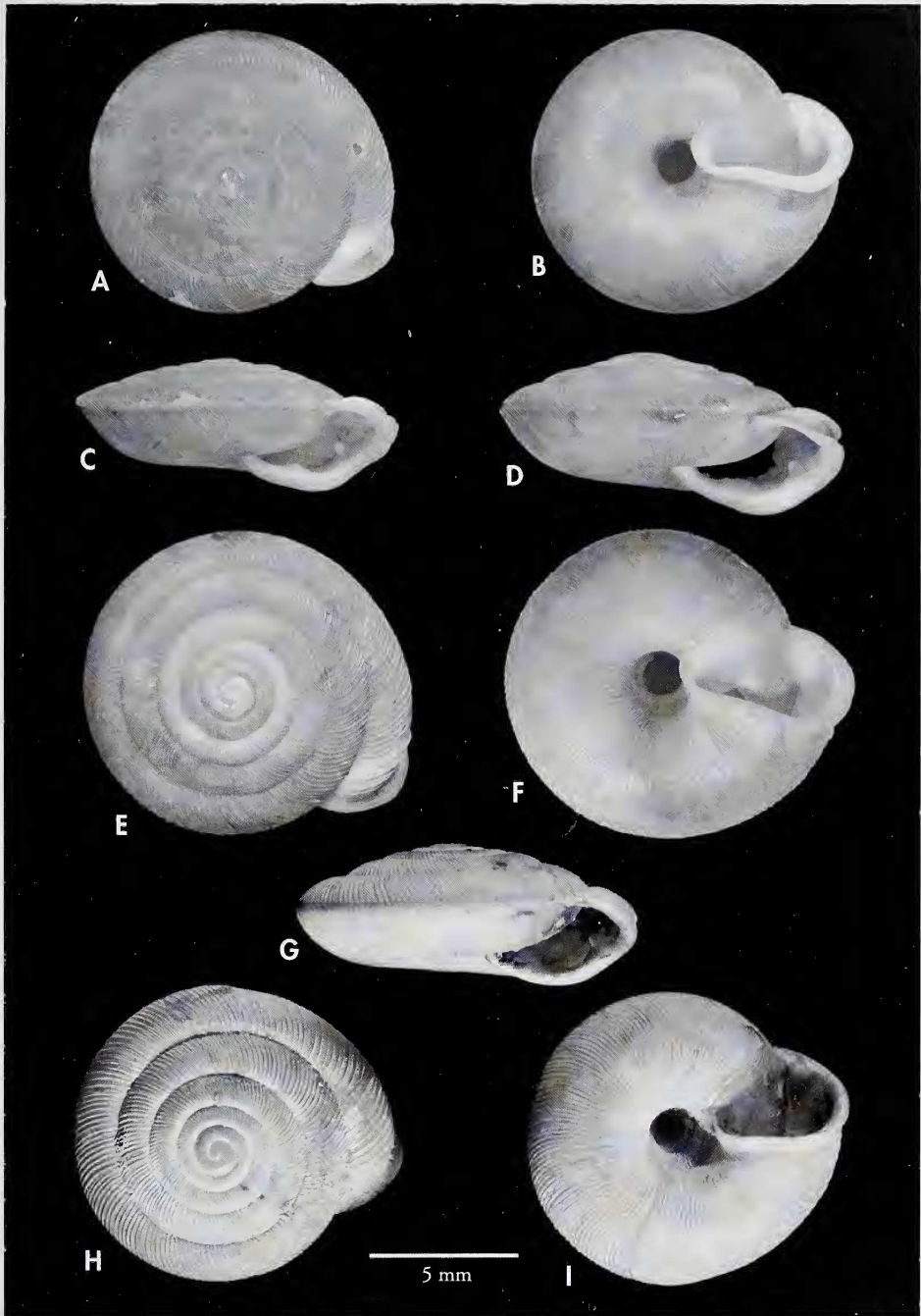


Figure 3. Shells of type material of *Oestophora barbula* (Rossmässler, 1838) and *O. barbella* (Servain, 1880). A-C: lectotype of *O. barbula* (SMF 7036); D-F: paralectotype of *O. barbula* (SMF 7035); G-I: lectotype of *O. barbella* (MHNG 17059A).

Figura 3. Conchas del material tipo de *Oestophora barbula* (Rossmässler, 1838) y *O. barbella* (Servain, 1880). A-C: lectotipo de *O. barbula* (SMF 7036); D-F: paralectotipo de *O. barbula* (SMF 7035); G-I: lectotipo de *O. barbella* (MHNG 17059A).

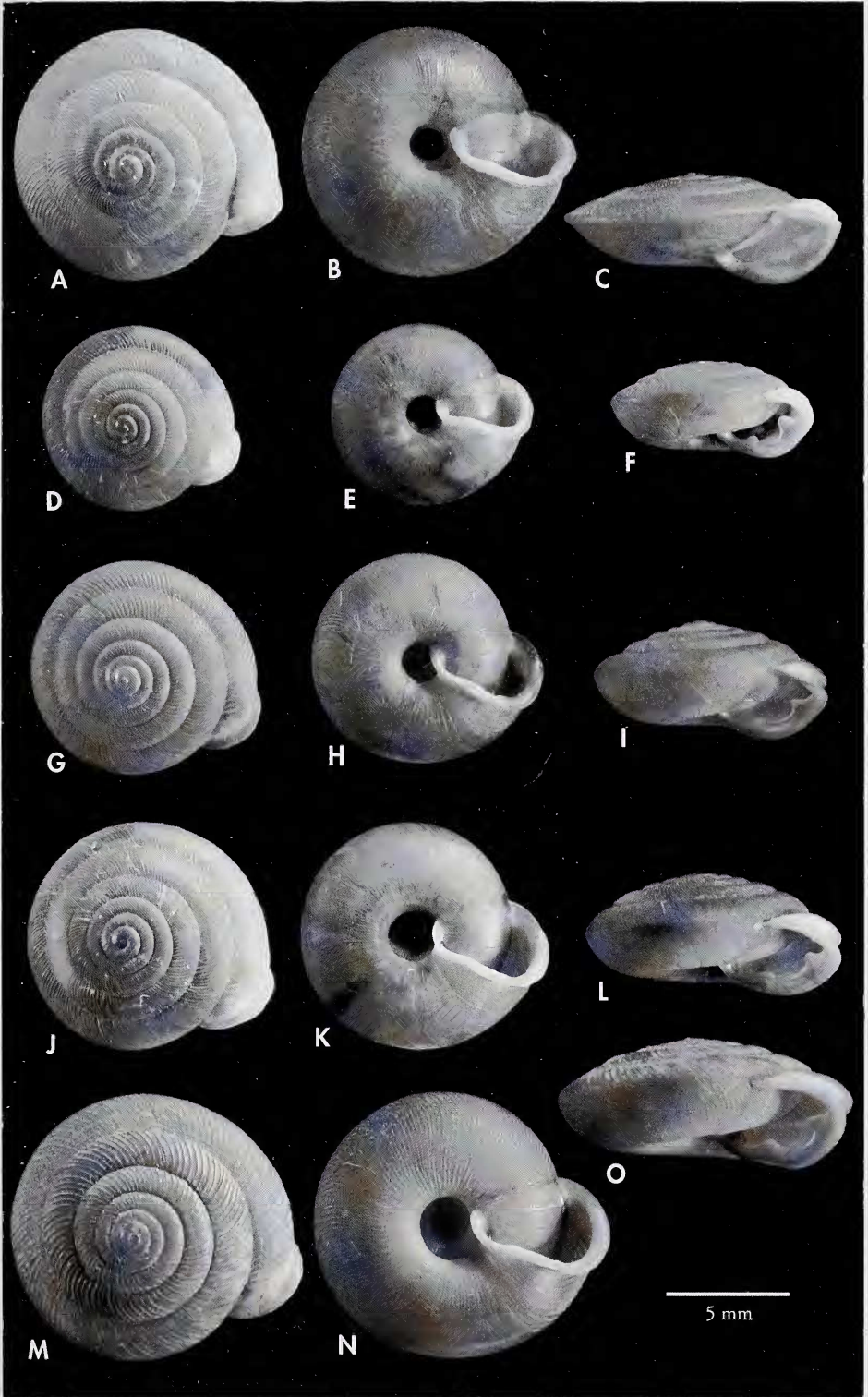
shell. The small papillae between the teleoconch ribs soon disappear in worn or corroded shells.

Geographical distribution. Records of *O. barbula* and *O. barbella* from Portugal are mapped in Figure 5. *O. barbula* confirmed by dissection was recorded only from western-central Portugal, from near Coimbra (Beira Litoral) southwards to the Serra da Arrábida (Estremadura), occurring inland only to the eastern limits of the limestone hills of SE. Beira Litoral, westernmost Beira Baixa and N. Ribatejo provinces. *O. barbella* has a much wider range, apparently throughout Portugal, since it is likely that the lack of records from much of Alentejo and parts of northern-central Portugal merely reflects sparsity of recent recording of land snails there. Since *O. barbula* appears to be endemic to Portugal, the many records mapped by PUENTE (1996: 87) for *O. barbula* [*sensu lato*] from western and southern Spain can probably all be referred to *O. barbella*. Her published figures of genital anatomy (PUENTE, 1996: 84-85) confirm *O. barbella* as occurring in the following Spanish provinces: Asturias, Cáceres, Huelva, Jaén, León, Lugo and Zamora. Many published figures of unkeeled shells from Spain also imply that *O. bar-*

bella occurs widely there. Unkeeled shells figured from the Azores (BACKHUYS, 1975), two shells seen from Terceira, Azores and figures of Madeiran shells (SEDDON, 2008) also strongly suggest it is *O. barbella* rather than *O. barbula* that occurs in these archipelagos, where it is likely to have been introduced by man. A population established near Driebergen, province of Utrecht, the Netherlands from at least 1994 to 2010 (DEES, 2011) also has unkeeled shells apparent from published photos. However, Quaternary fossil specimens from Mallorca that have been reported as *O. barbula* are now reinterpreted as an extinct endemic species named as *Darderia bellverica* by ALTABA (2006).

Habitat preferences. Descriptions of habitats where the present authors collected specimens of known identity (mainly confirmed anatomically) were recorded from 2001-2011 at 81 localities in Portugal or neighbouring provinces of Spain. Only one locality had both species living together (see next section). Both species occur mainly in the lowlands and on low hills. Altitudinal ranges were recorded for *O. barbula* as ca 13 m (1 km SW. of Alfarelos, Beira Litoral) to 548 m (high on Serra de Sico, Beira Litoral); for *O. barbella* as 7-10 m (on coastal sand du-

(Right page) Figure 4. Shells of (A-F) *Oestophora barbula* (Rossmässler, 1838), (G-I) *O. cf. barbula* and (J-O) *O. barbella* (Servain, 1880) to show variability between populations. A-C: 19 July 2010, ca 1 km SW. of Serro Ventoso, Estremadura, from restricted type locality; D-F: 12 Feb. 2011, Serra da Arrábida, Estremadura (29SNC020602), from population coexisting with *O. barbella*, see Figures 4J-L; G-I: 4 June 2011, 2 km NNE. of S. Pedro de Moel, Estremadura, from apparently atypical population of *O. barbula* with small unkeeled shells; J-L: 12 Feb. 2011, Serra da Arrábida, Estremadura (29SNC020602), from population coexisting with *O. barbula*, see Figures 4D-F; M-O: 3 Nov. 2010, NW. of Verride near Rio Mondego, Beira Litoral, from population with shell keel more developed than in most *O. barbella* (all specimens in Collection of G.A. and D.T. Holyoak). (Página derecha) Figura 4. Conchas de (A-F) *Oestophora barbula* (Rossmässler, 1838), (G-I) *O. cf. barbula* y (J-O) *O. barbella* (Servain, 1880) para mostrar la variabilidad entre poblaciones. A-C: 19 jul. 2010, aproximadamente 1 km. SO de Serro Ventoso, Estremadura, de la localidad-tipo restringida; D-F: 12 feb. 2011, Serra da Arrábida, Estremadura (29SNC020602), de la población conviviendo con *O. barbella*, véase Figuras 4J-L; G-I: 4 jun. 2011, 2 km. NNE de S. Pedro de Moel, Estremadura, de la población aparentemente atípica de *O. barbula* con pequeñas conchas sin quilla; J-L: 12 feb. 2011, Serra da Arrábida, Estremadura (29SNC020602), de la población conviviendo con *O. barbula*, véase Figuras 4D-F; M-O: 3 nov. 2010, NO. de Verride cerca de Rio Mondego, Beira Litoral, de la población con la quilla de la concha más desarrollada que en la mayoría de *O. barbella* (todos los ejemplares en la colección de G.A. y D.T. Holyoak).



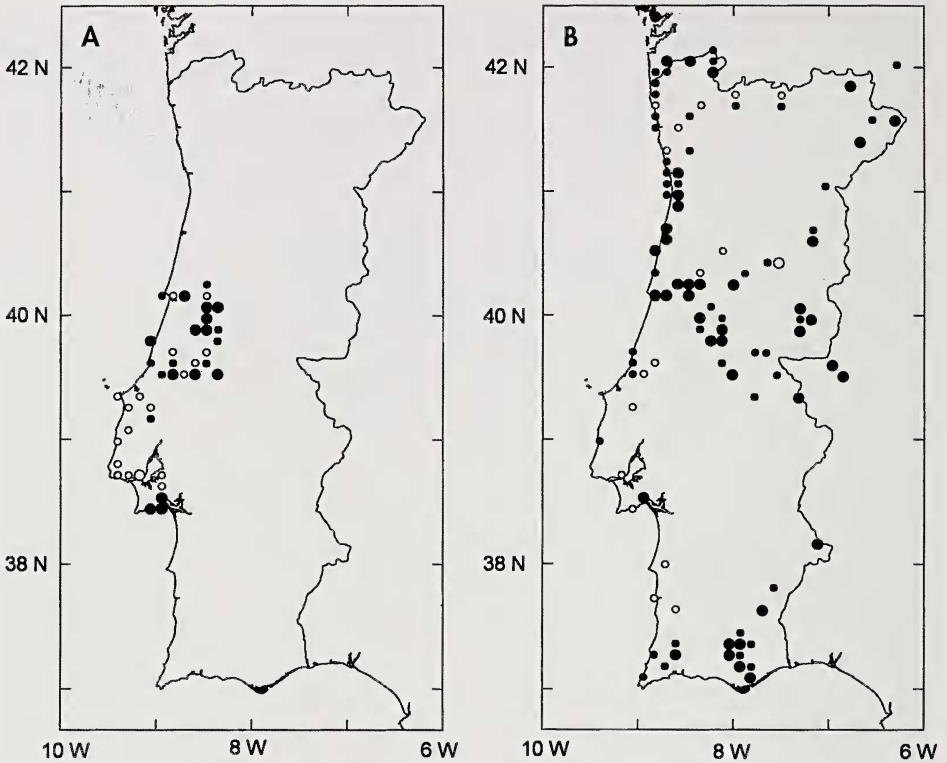


Figure 5. Distribution of (A) *Oestophora barbula* (Rossmässler, 1838) and (B) *O. barbella* (Servain, 1880) in Portugal and adjoining regions of Spain. ●: collected since 1999 by authors or Álvaro De Oliveira, confirmed by dissection; ●: collected since 1999 by authors or Álvaro De Oliveira, shells only; ○: collected before 2000, confirmed by dissection (HESSE, 1931 or CASTILLEJO ET AL., 1987); ○: collected before 2000, shells only (mainly confirmed by Álvaro De Oliveira).

Figura 5. Distribución de (A) *Oestophora barbula* (Rossmässler, 1838) y (B) *O. barbella* (Servain, 1880) en Portugal y en las regiones cercanas de España. ●: recogidos desde 1999 por los autores o por Álvaro de Oliveira, confirmados por la disección; ●: recogidos desde 1999 por los autores o por Álvaro de Oliveira, sólo conchas; ○: recogidos antes de 2000, confirmados por la disección (HESSE, 1931 o CASTILLEJO ET AL., 1987); ○: recogidos antes de 2000, sólo conchas (principalmente confirmados por Álvaro de Oliveira).

nes) up to 890 m (Foia, Algarve), 1015 m (near summit of Pico São Mamede, Alto Alentejo), 1050 m (Sabugeiro, Beira Alta) and at least 1080 m (N. of Lamas de Mouro, Minho). Both species were recorded in wooded and open sites, living specimens most often being found resting beneath substantial boulders.

O. barbula was found at 21 localities, 20 of which were on bedrock of Cretaceous or Jurassic limestone, mainly where the rock was exposed in crags or as limestone pavements or large boulders, but predominantly in dry-stone walls at

a few sites. At a single locality (ca 2 km NNE. of Santa Cita, Ribatejo) it was found living on alluvial banks of a lowland river, albeit within a river catchment having much limestone bedrock. At the latter locality limestone boulders had been imported to provide protection for parts of the river bank, so it is possible that *O. barbula* reached the site with these or that it arrived there by drifting down the river. Possible occurrence of a second population of this species in a different habitat (at site P67/P161) is discussed above.

O. barbella was recorded at 60 localities, over a much wider range of rock types than those where *O. barbula* was found, including acidic lithologies. Sedimentary rock types characterised less than half of the localities, with records from sites with exposed limestone rock (10 sites; 16.7%), man-made banks of limestone boulders (2 sites; 3.3%), sandstone (3 sites; 5.0%), and unconsolidated sediments of calcareous sand in coastal dunes (8 sites; 13.3%) and sands and gravel capping limestone near the coast (1 site; 1.7%). A majority of records were from localities with various metamorphic rocks, recorded as slates (mainly Paleozoic) (11 sites; 18.3%), slate and shale (2 sites; 3.3%), slate and schist (3 sites; 5.0%), slate and quartzite (1 site; 1.7%), quartzite (5 sites; 8.3%), granite (11 sites; 18.3%) and Foiaite (2 sites; 3.3%). The single remaining site (1.7%) was along a concrete roadside wall with no rock exposed nearby. Some sites with *O. barbella* were more disturbed by man than those tolerated by *O. barbula*, including edges of cultivated land and managed road verges.

It is noteworthy that although *O. barbella* was recorded at 12 sites with limestone rocks, as noted above, the species was normally absent from places with exposed Cretaceous or Jurassic limestone within the range of *O. barbula* (i.e. from Lisbon north to around Coimbra: Fig. 5). Nevertheless, over that extensive region *O. barbella* was found on man-made banks of limestone boulders near rivers (2 sites) and on coastal dunes (3 sites), so it appears to either avoid the rocky sites with natural Mesozoic limestones or to be excluded from them by the presence of the relatively common *O. barbula*. Further evidence that competitive exclusion might occur is that outside the range of *O. barbula*, *O. barbella* was found to occur widely on outcropping Mesozoic limestone. In the Algarve it was usually found (7 sites) at much lower density than the accompanying *Gittenbergeria turriplana* (Morelet, 1845) (Trissexodontidae), an Algarve endemic with a larger sharply keeled shell; it was also found among hard

limestone rocks in the Serra de la Encina (Prov. Ourense) (1 site). Where *O. barbella* meets the southern edge of the range of *O. barbula* in the Serra da Arrábida (Estremadura), *O. barbella* was found alone at one site (in plenty), *O. barbula* was found alone (in plenty) at two sites and both species coexisted at a fourth site, as follows.

Coexistence of O. barbula and O. barbella. Although the ranges of *O. barbula* and *O. barbella* approach closely and probably interdigitate around Coimbra and Figueira da Foz (Beira Litoral), they were not found living together and their records were from different habitats, as described above. However, at one of four sites studied on the Serra da Arrábida (P129 at 29SNC020602) the two species were found living together, at 380-388 m altitude on N-, NW. and S-facing rocky limestone slopes with patches of scrub. Visits on 17 May 2007 and 12 February 2011 amassed 22 adult *O. barbula* (4 living, 18 shells) and 16 adult *O. barbella* (8 living, 8 shells) from within a 100 metre radius, both species twice being found together alive under a single boulder. The same two visits to the Serra da Arrábida revealed *O. barbella* occurring alone at one site (P128 at 29SNC032604, 45 adults, from rocky limestone hilltop with low scrub) and *O. barbula* occurring alone at two other sites (P130 at 29SMC999576 to 29SNC000577, 68 adults, limestone road-cutting, scree and slope with tall scrub locally; P131 at 29SNC01175874, 12 adults, roadside at base of cutting in limestone rock). The identity of specimens from all four sites was confirmed by study of the epiphallus (in several individuals from three sites, one from the fourth) and all adult shells were easily separated by the presence of a sharp peripheral keel in *O. barbula* alone (cf. Figs. 4D-F and 4J-L).

It is noteworthy that at these four sites in the Serra da Arrábida shell size of both species is rather similar where each occurs alone, but it diverges markedly where the two species coexist (Table II, Figs. 4D-F and 4J-L). Thus, mean shell breadth for *O. barbella* occurring alone (site P128) is 9.58 mm, and

for *O. barbula* occurring alone it is 9.65 mm (site P130) and 10.34 mm (site P131). At site P129 with both species living together, *O. barbella* is larger at 10.63 mm whereas *O. barbula* is smaller at 8.51 mm.

Based on data listed in Table II, statistical significance of the differences among sample means for shell breadth was calculated pair-wise for sites P128-P131. After it was established with Snedecor's *F* that there is no significant difference of the respective variance ratio between each of the pair of samples compared ($p > 0.05$), values of Student's *t* were calculated applying Bessel's correction. These results confirm that at site P129 *O. barbula* is smaller than at neighbouring sites (P130: $t = 8.94$, 86 d.f., $p < 0.001$; P131: $t = 8.47$, 31 d.f., $p < 0.001$) whereas *O. barbella* is larger than at a neighbouring site (P128: $t = 6.18$, 42 d.f., $p < 0.001$); they also confirm the size difference between the two species at site P129 ($t = 3.02$, 36 d.f., $p < 0.01$).

Furthermore, the small size of *O. barbula* at site P129 appears to be a special effect of sympatry with *O. barbella* rather than due to chance alone, since this is much the smallest of 30 populations of *O. barbula* encountered anywhere in this study (cf. Table II), with the possible exception of specimens from P67/P161 (see above) which have unkeleled shells and somewhat ambiguous genital anatomy so some doubt remains about the species identification.

These differences in shell size between the two species are suggestive of the phenomenon of "character displacement" (BROWN AND WILSON, 1956; PIANKA, 1974), which refers to increased differences between species where they occur together. It is argued that in such cases selective pressures from interspecific competition have tended to maximise the differences in size and hence in resource utilisation among coexisting species (BROWN, 1975; DIAMOND, 1975). This presumes that differences present in sympatry are inherited and allow an evolutionary response. FENCHEL (1975) proposed this explanation for size differences developed between some mud-snail

species (Hydrobiidae) only when they coexist, but SALONIEMI (1993) proposed an environmental explanation whereby only those habitat types able to support two coexisting mud-snail species allow one of the species to grow large. Subsequently, experimental studies by GORBUSHIN (1996) pointed to the size differences in sympatry being an effect of direct competition for food, affecting one of the species more than the other, not an inherited adaptive response. In fact, most examples of "character displacement" involve birds or other vertebrates where size differences in adults of two species can allow partitioning of resources. As pointed out by HYLLEBERG (1976) and stressed by GORBUSHIN (1996) it is unlikely that coexisting species of snail can partition resources in the same manner because a large part of their populations will be comprised of immatures that show extensive size overlap between species. Hence, "character divergence" in sympatric snails may be evidence of interspecific competition, but need not involve inherited size differences.

TAXONOMIC DISCUSSION

Authorship, lectotypification and type-locality of *O. barbula*

HIDALGO (1875: 42) cited the name *Helix bituberculata* A. Férussac, 1837, from the catalogue published in Paris for the sale of the Férussac Collection (on p. 4, from Portugal). This name was evidently a *nomen nudum* that Hidalgo interpreted as representing [*Helix*] *barbula* Charpentier.

ROSSMÄSSLER (1838: 11, Taf. 32, Fig. 451) gave the first description and figures of the species, as *Helix barbula* v. Charp., with "Syn. *Helix barbula* v. Charp. in litt." also listed. Subsequently, HESSE (1931: 52) listed the authorship of the name as "*Oestophora barbula* (Chrp.) Rssm." and ORTIZ DE ZÁRATE LOPEZ (1962: 91), CASTILLEJO (1984: 128) and CASTILLEJO ET AL. (1987) all adopted "*Oestophora (Oestophora) barbula* (de Charpentier)". However, PUENTE (1996: 82) accepted Rossmässler as author and

this appears to be correct on the basis that Charpentier presumably provided the name whereas Rossmässler was responsible for the description, so only the latter can be regarded as the author responsible for its naming.

The collection of the Forschungsinstitut Senckenberg contains two shells labelled as those of *Helix barbula* figured by Rossmässler (*loc. cit.*), one more sharply keeled (SMF 7036, shell diameter 11.1 mm: Figs. 3A-C) than the other (SMF 7035, diameter 11.9 mm: Figs. 3D-F). SMF 7035 had been labelled as "lectotype" by the late Dr. Adolf Zilch, but the designation is invalid since it was never published. Close study of Rossmässler's fig. 451 (*loc. cit.*; especially the first of the four figures) suggests the figured specimen was actually the more sharply keeled SMF 7036. Since SMF 7036 also shows the clearest development of the shell keel characteristic of the taxon with a large epiphallus from western-central Portugal this shell is selected here as lectotype, leaving SMF 7035 as a paralectotype.

ROSSMÄSSLER (1838: 11) recorded the provenance of the type material as "von Holl auf seiner Aktien-reise in Portugal gesammelt". Searches have produced no additional information to indicate a more precise locality. This is unfortunate because a small proportion of shells of *O. barbella* appear indistinguishable from the lectotype of *O. barbula*. We cannot designate a neotype for *O. barbula* based on a specimen with large penial epiphallus because undoubted syntype shells still exist (ICZN Art. 75(a)). Although the ICZN could itself set aside the existing type material and designate a neotype under its plenary powers if a detailed application were to be made (Recommendation 75E), it would need to be demonstrated that such action "is essential for solving a complex zoological problem" (Art. 75). MAYR (1969: 375, 56.B.3) concluded that "in most cases [of this type] no such neotype designation will be needed", adding (MAYR, 1969: 374-375, 56.B.3) that the ICZN Code "contains no provisions regarding what to do when the type lacks all diagnostic characters".

A convenient solution to this problem lies in restricting the type-locality, which was given only as "Portugal" in the original description of *O. barbula* and has never before been restricted, either directly, or by our designation of a lectotype. Following ICZN Recommendation 72H on restricting type localities, only its section (4) can be applied: "as a last resort, and without prejudice to other clarification, localities within the known range of the taxon or from which specimens referred to the taxon had been taken". Hence we restrict the type-locality of *O. barbula* to "limestone crags ca 1 km SW. of Serro Ventoso, S. of Porto de Mós, Estremadura, in central Portugal". This locality excludes any likelihood of *O. barbella* being present, whereas anatomically verified *O. barbula* with large keeled shells (Figs. 4A-C) resembling that of the lectotype are abundant there. Although this action is arbitrary with respect to Rossmässler's material, a first reviser may designate a restricted type locality. Such a restriction may later be set aside if it conflicts with the available evidence, but only if the case is unequivocal (MAYR, 1969: 377, note 2).

Authorship and lectotypification of *O. barbella*

Type specimens of *Helix barbella* (SERVAIN, 1880: 66) were studied on loan from Muséum d'Histoire Naturelle, Ville de Genève (MHNG). These notes describe this material, set out reasons for believing that it forms all or part of the original "type series" and provide a background to selection of a lectotype for the species.

The type material studied comprised two similar corked glass tubes with round bases, each of them labelled on the outside with a blue edged label annotated as follows in ink:

Helix barbella Servain Mertola Portugal [11 shells; subsequently numbered at MHNG as 17059; cork with 51. written in ink].

Helix barbella Servain Lisbonne [1 shell; subsequently numbered as 17060; cork with 34. written in ink];

These two tubes are contained in a small card box that is glued to a larger wooden base. A label pasted on the bottom of the inside of the box states: *Helix Barbella*, Bourguignat in: Servain, Cat. Moll. Esp. p. 1880. A label pasted outside the box on the top of the wooden base has printed "Muséum de Genève Collection Bourguignat" and hand-written *Helix barbella* Bgt. [Localité] Portugal.

The box and its two labels evidently date from the curation of the material as part of Bourguignat's collection at MHNG. Their attribution of authorship to Bourguignat is probably erroneous because the labels on the two tubes give only Servain as author of the name, and this is in agreement with the original publication having Servain as sole author and also the original description making no mention of Bourguignat.

It can be inferred that these specimens from Bourguignat's collection form all or part of Servain's "type series" of *Helix barbella* for the following reasons, which taken together, leave no real doubts:

(1) The original collection of G. Servain has apparently not survived intact. At least, the list of collections by DANCE (1986: Appendix IV) makes no mention of it.

(2) There is clear evidence that Servain worked closely with Bourguignat and apparently made at least some of his Spanish and Portuguese specimens available to him. The book by SERVAIN (1880: 6) makes a lavish acknowledgement of Bourguignat (and no other collaborator) stating: "à notre excellent ami M. J. R. Bourguignat, nos remerciements pour son extrême obligeance, qui ne s'est jamais démentie à notre égard, et pour la complaisance avec laquelle il a bien voulu nous éclairer sur la valeur de nos espèces et mettre à notre disposition sa riche bibliothèque et son immense collection."

(3) Types of other Portuguese snails described in SERVAIN (1880) appear to be in the Bourguignat collection. Thus, in dealing with *Candidula*, GITTENBERGER (1993: 283) points out that "Topotypes of

nominal taxa described by G. Servain, found in the collection of J.R. Bourguignat, might in fact be syntypes donated by their author."

(4) The two localities given in the original description of *H. barbella* (SERVAIN, 1880: 67) and those on tubes in the Bourguignat collection correspond exactly and the number of specimens from each of them also corresponds well. Thus, Servain wrote "Alluvions du Tage près de Lisbonne, où elle est rare. – Elle est assez abondante, à ce qu'il paraît, aux alentours de Mertola en Portugal." The material of *H. barbella* in Bourguignat's collection comprises just two tubes, respectively from "Lisbonne" [1 shell] and "Mertola" [11 shells].

(5) The characters of the shells in the Bourguignat collection show unusual features which correspond exactly to parts of Servain's original description. Thus, SERVAIN (1880: 67) states that there is only a single palatal tooth ("*orné seulement d'une grosse dent vers la région médiane du borde externe*": italics as in original). The Mertola material at MHNG (11 shells) has one shell with only a single tooth (outer palatal only), four shells giving a superficial impression of having only a single tooth (with a very weak or weak and rather inconspicuous inner tooth), one shell with the inner tooth almost obscured by the dried body; hence only the remaining five shells have a conspicuous and strong inner palatal tooth. The single shell at MHNG from "Lisbonne" also has only a small, weak inner palatal tooth. Occurrence of only a single palatal tooth is recurrent but rare in populations of the *O. barbula*/*O. barbella* group of taxa (ORTIZ DE ZÁRATE LOPEZ, 1962; CASTILLEJO ET AL., 1987; PUENTE, 1996).

In the original description, SERVAIN (1880: 67) also stated that the shell has "*son dernier tour aussi fortement lamellé en dessous qu'en dessus*" (italics as in original), i.e., the body whorl has ribbing on the underside as strong as that on the upperside. Ribbing in the MHNG material is present on the underside of all 12 shells and strong in some of them; five of the shells from Mertola have the ribbing

on the underside as strong or nearly as strong as that on the upperside. Generally, ribbing of shells in this species-group is rather variable, but it is infrequently as strong on the underside of the body whorl as it is on the upperside.

(6) The condition of the shell at MHNG from "Lisbonne" corresponds to the "Alluvions du Tage" of the original description: it is encrusted with silt on the outside of the spire and inside the shell mouth.

Overall, it seems there can be no certainty that all of Servain's original "type series" is now in the Bourguignat collection. However, the evidence that at least part of it is present there is compelling. Since the original Servain collection of shells no longer appears to exist, there is thus ample justification for selecting a lectotype from the Bourguignat collection at MHNG.

Therefore, a lectotype is designated here to fix application of the name *Helix barbella* Servain, 1880. The lectotype selected is from Mertola (i.e. Mértola) and is placed in a separate small tube and labelled as MHNG 17059A (Figs. 3G-I); it measures 11.2 mm in diameter, 4.5 mm in height and has 5.6 whorls, a weak inner palatal tooth and strong ribbing on the underside of the shell; traces of the body and dark staining suggest the animal was alive when collected. Ten paralectotypes from Mértola remain in the original tube (as 17059B); these have shell diameter 9.2-11.3 mm (mean 10.33, s.d. 0.79 mm), shell height 3.8-4.9 mm (mean 4.29, s.d. 0.39 mm), 4.8-5.7 whorls (mean 5.27, s.d. 0.24 whorls). One paralectotype from "Lisbonne" (17060) remains in its original tube; it has shell diameter 10.1 mm, shell height 4.7 mm and 5.4 whorls. All the shells of the "type series" of *O. barbella* have a rounded keel on the body whorl, less sharp than in either of the two syntypes of *O. barbula* Rossmässler.

The genital anatomy has been studied from two specimens of *O. barbella* collected recently at Mértola (20 Oct. 2008, Cerrinho das Neves, Mértola (29SPB1767), Mértola, Baixo Alentejo, leg. Álvaro De Oliveira; Collection of G.A.

and D.T. Holyoak); both show a relatively short and weak penial epiphallus (Fig. 2H). The shells from these two specimens have been compared with the lectotype and ten paralectotypes from Mértola, which they resemble in the rounded keel on the body whorl and general form of the shell. These two recently collected shells are within the range of variation of the paralectotypes in their shell dimensions, weak/medium strength of ribbing on underside of body whorl and the medium/strong inner palatal tooth.

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APPENDIX. MATERIAL STUDIED.

Data are listed in sequence as country, province, locality name, habitat description, altitude, U.T.M. grid reference, date (YYYY.MM.DD), collector(s) followed by – then collector's field number, number of specimens, number of shells, collection, museum registration number, comments; successive entries are separated by semi-colons. Abbreviations: ÁDO = Álvaro De Oliveira, CGAH = Collection of G.A. and D.T. Holyoak, DTH = D.T. Holyoak, GAH = G.A. Holyoak, leg. = collected by, MHNG = Muséum d'histoire Naturelle, Ville de Genève, Switzerland, SMF = Forschungsinstitut Senckenberg, Germany, sh = number of intact adult shells (without preserved bodies), sp = total number of adult specimens with bodies preserved in alcohol (number of dissected adult specimens is given in parentheses).

O. barbella, Portugal, Algarve: *ca* 0.5 km S. of Bensafrim, base of N.-facing limestone crag, 76 m, 29S 05237/41116, 2011.02.06, GAH and DTH – P121, 2 sh, CGAH; W. slope of Foia, hillslopes with low metamorphic crags (Foyaite) and patchy cover of *Erica* and *Cistus*, grassland locally, 810 m, 29S 05347/41292, 2011.02.05, GAH and DTH – P120, (1) sp, CGAH; *ca* 0.5 km E. of summit of Foia (W. of Monchique), hilltop with blocks of metamorphic rock amongst low scrub, *ca* 890 m, 29SNB33, 2001.06.03, GAH, 5 sh, CGAH; E. end of Rocha da Pena, rocky limestone slope and plateau with patches of bushes, 460 m, 29S 05803/41234, 2011.01.28, GAH and DTH – P104, (1) sp, 4 sh, CGAH; E. end of Rocha da Pena, rocky limestone slope with patches of tall bushes, 462 m, 29S 058033/412344, 2011.01.31, GAH and DTH – P112, (1) sp, CGAH; by N2 at 4.5 km NW. along road from Ameixial, roadside cutting with steep slaty/shaley rock and patchy low herbs and grasses, 265 m, 29S 05898/413885, 2011.01.30, GAH and DTH – P110, (1) sp, 7 sh, CGAH; *ca* 2 km E. of Santa Barbara de Nexe, rocky limestone hill-slopes with patchy low scrub, 261 m, 29S 059428/410732, 2011.02.03, GAH and DTH – P117, 1 sh, not kept; by N2 NNW. of Alportel, rocky (slate and sandstone) slopes in open *Pinus*, *Quercus* and *Eucalyptus* woodland by road, 365 m, 29S 059569/411731, 2011.01.28, GAH and DTH – P106, (2) sp, 9 sh, CGAH; by N124 W. of Quintã, banks and steep bases of road cuttings in slaty/schist rock, with sparse *Cistus*, grasses and herbs, 211 m, 29S 059037/412121, 2011.01.31, GAH and DTH – P113, 1 sh, CGAH; by N2 S. of Ameixial, steep slaty/shaley roadside cuttings with sparse patches of grasses and herbs, 406 m, 29S 059164/413483, 2011.01.30, GAH and DTH – P111, (1) sp, CGAH; by N398 *ca* 2 km N. of Moncarapacho, limestone slope with low rocks and patches of scrub, *ca* 121 m, 29S 06068/41078, 2011.01.29, GAH and DTH – P108, (1) sp, 1 sh, CGAH; Serra de São Miguel (*ca* 4 km NW. of Moncarapacho), rocky limestone slopes with patchy scrub and grassland, 340 m, 29S 06043/41067, 2011.02.04, GAH and DTH – P119, (1) sp, 7 sh, CGAH; *ca* 3 km NNW. of Moncarapacho (just S. of A22), rocky limestone hillslope with patchy bushes, 131 m, 29S 060695/410771, 2011.02.04, GAH and DTH – P118, (1) sp, 1 sh, CGAH; just NW. of Barroqueira (*ca* 7 km NW. of Moncarapacho), rocky limestone slopes and quarries with patchy bushes, 183 m, 29S 060291/411092, 2011.01.29, GAH and DTH – P107, 2 sh, CGAH; Alto Alentejo: Belver castle, Gavião, 29SND8972, 2008.11.21, ÁDO, (3) sp, CGAH; by Rib. de Sor *ca* 4 km NW. of Monte da Pedra (NW. of Crato), granite rocks with sparse scrub near river, *ca* 183 m, 29SPD05, 2001.05.30, GAH, 7 sh, CGAH; N. end of Barragem da Povia, granite walls and rocks in deciduous grove on reservoir margin, 320 m, 29SPD27, 2001.05.31, GAH, 1 sh, CGAH; Pico São Mamede, beneath boulders on sparsely vegetated N.-facing hillside near crags, *ca* 1015 m, 29S 06413/43527, 2007.05.15, GAH – 2007.5, (1) sp, 3 sh, CGAH; Azores: Duque da Terceira Garden, Angra do Heroísmo, Ilha Terceira, 26NMH87, 2005.11.01, ÁDO, 2 sh, CGAH; Baixo Alentejo: by N2 at *ca* 1.5 km SSE. of Dogueno, unshaded road cuttings with exposed sandstone, sparse low vegetation, 338 m, 29S 059045/414242, 2011.01.30, GAH and DTH – P109, 2 sh, CGAH; Cerrinho

das Neves, Mértola, 29SPB1767, 2008.10.20, ÁDO, (2) sp, CGAH; Noudar Castle, Barrancos, 29SPC6927, 2008.10.19, ÁDO, (3) sp, CGAH; Mertola, G. Servain, 1 sh, MHNG 17059A, Lectotype, 10 sh, MHNG 17059B, Paralectotypes; Beira Alta: Sabugeiro, bases of low granite crags and walls near river, 1050 m, 29T 06149/44733, 2010.08.31, GAH and DTH – P71, 3 sh, CGAH; by N16 on W. edge of Gonçalbocas, granitic slopes with much bare rock, patchy herbs and grasses, bushes locally, 814 m, 29T 065385/449325, 2011.10.14, GAH and DTH – P209, (3) sp, 7 sh, not kept; W. edge of Moinhos de Aveia (W. of Alverca da Beira), rocky granitic slopes with patchy low scrub, 554 m, 29T 06518/45071, 2011.06.26, GAH – P165, 1 sh, not kept; Beira Baixa: *ca* 1.5 km W. of Lousa (S. of Vila de Rei), rocky (quartzite and slaty) slopes with patchy scrub and few trees, 210 m, 29S 05747/43862, 2011.07.27, GAH and DTH – P174, 1 sh, not kept; by Rio Zêzere and N238 ENE. of Dornes, rocky (slate) cuttings and slopes by road and reservoir, building ruins, 143 m, 29S 05644/44037, 2011.08.05, GAH and DTH – P177, (2) sp, 28 sh, CGAH; Barcoila, near Sertã, garden walls, *ca* 410 m, 29S 05741/44096, 2010.09.11, GAH – P72, (1) sp, 6 sh, CGAH; W. edge of Sertã, under cardboard on roadside verge with patchy herbs, *ca* 240 m, 29S 05769/44065, 2010.04.22, GAH – P37, (3) sp, 2 sh, CGAH; Rio Zêzere valley W. of Pedrógão Pequeno, rocky granitic slopes of valley side with open *Pinus* and *Quercus* woodland, *ca* 250 m, 29S 05737/44176, 2011.04.27, GAH and DTH – P140, (2) sp, CGAH; by Rio Ocreza and N241 E. of Vale da Mua, grassy banks near river, 29S 060554/439514, 2008.08.21, GAH – P6, 1 sh, not kept; Portas de Almorão, rocky (quartzite) slopes with patchy scrub and herbs, 275 m, 29S 060681/439902, 2010.12.19, GAH and DTH – P86, 15 sh, CGAH; *ca* 2 km W. of Vila Velha de Ródão, rocky (quartzite) ridge and slopes with patchy low scrub and herbs, 321 m, 29S 061177/439016, 2010.12.19, GAH and DTH – P87, 5 sh, CGAH; by N240 on W. bank of Rio Ponsul (W. of Ladoeiro), S.-facing rocky (sandstone) banks/cutting with patchy scrub and grasses, 183 m, 29S 064235/0441332, 2010.12.23, GAH and DTH – P88, (3) sp, 12 sh, CGAH; by N233 *ca* 3 km W. of Oledo, rocky (granite) slopes by road and river, with patches of trees and scrub, 260 m, 29S 06413/44263, 2011.01.15, GAH and DTH – P99, 1 sh, CGAH; by N353 just SE. of Idanha-a-Nova, rocky (granite) hillside with patches of scrub and low trees, 288 m, 29S 065144/442069, 2010.12.27, GAH and DTH – P95, (1) sp, 4 sh, CGAH; by N239 just SW. of Proença-a-Velha, rocky (granite) slopes by road and river, with patches of trees and scrub, 375 m, 29T 064964/443134, 2011.01.15, GAH and DTH – P100, (3) sp, 5 sh, CGAH; Beira Litoral: Casal de São Simão, NE. of Aguda, quartzite crags and slopes, grassland, walls of chapel, 385 m, 29S 05562/44188, 2011.09.06, GAH and DTH – P192, 5 sh, not kept; *ca* 2 km NE. of Favacal, quartzite rocks and slopes of hilltop, with grassland, bushes and concrete walls, 755 m, 29S 05576/44272, 2011.09.06, GAH and DTH – P191, (1) sp, not kept; *ca* 1 km N. of Pedrogão Grande, deciduous groves by stream, roadsides, rocky banks, walls, 330 m, 29S 057223/442063, 2011.08.11, GAH and DTH – P179, 3 sh, not kept; just S. of S. Pedro (S. of Figueira da Foz), coastal sand dunes with patchy low scrub, *ca* 10 m, 29T 05117/44412, 2011.01.13, GAH – P97, (3) sp, 11 sh, CGAH; Praia da Tocha, sand dunes with patches of low bushes, 14 m, 29T 05134/44647, 2010.11.18, GAH and DTH – P83, 2 sh, CGAH; *ca* 1 km NW. of Gafanha do Areão (SW. of Aveiro), sand dunes, with much *Acacia* scrub, 8 m, 29T 05188/44862, 2010.10.26, GAH – P76, (3) sp, 28 sh, CGAH; *ca* 1 km NW. of Verride near Rio Mondego, grassy banks with limestone boulders locally, 11 m, 29T 05244/44437, 2010.11.03, GAH and DTH – P78, 10 (4) sp, CGAH; just S. of Costa Nova do Prado, sand-dunes with patchy herbs and low shrubs, 7 m, 29T 05209/44948, 2011.05.03, GAH and DTH – P144, (3) sp, 4 sh, CGAH; Vista Alegre, Ílhavo, 29T NE2793, 2009.10.26, ÁDO, (1) sp, CGAH; N. of Ameal, grassland and limestone boulders on bank of river, *ca* 12 m, 29T 05393/44502, 2010.11.03, GAH and DTH – P80, 11 (4) sp, 12 sh, CGAH; Quinta das Lágrimas, Coimbra, 29TNE4849, 2010.05.11, ÁDO, (1) sp, CGAH; Botanical Garden, Coimbra, 29TNE4950, 2009.03.10, ÁDO, (3) sp, 1 sh, CGAH; Instituto Geofísico, Coimbra, 29TNE5051, 2009.11.20, ÁDO, (1) sp, CGAH;

Coja, Arganil, 29TNE8658, 2009.11.02, ÁDO, (1) sp, CGAH; S. Jacinto, Aveiro, 29TNF2303, 2008.08.30, ÁDO, (1) sp, CGAH; Cais do Puchadouro, Ovar, 29TNF3120, 2009.11.20, ÁDO, (1) sp, CGAH; Feira castle, Santa Maria da Feira, 29TNF3830, 2008.12.12, ÁDO, (3) sp, CGAH; Douro Litoral: just E. of São Félix da Marinha, walls and plantation with *Eucalyptus*, ca 105 m, 29T 05330/45424, 2007.05.20, GAH – 2007.17, 29 sh, CGAH; Botanical Garden, Porto, 29TNF3056, 2008.10.07, ÁDO, (3) sp, CGAH; Scarp over Douro River, Porto, 29TNF3354, 2008.01.14, ÁDO, (3) sp, CGAH; Estremadura: ca 1 km W. of Cela Velha (ca 6 km S. of Nazaré), roadsides, grassland and grove of *Populus*, ca 9 m, 29S 049419/437824, 2011.06.04, GAH and DTH – P164, 1 sh, not kept; just E. of lighthouse at Nazaré, sandy and gravelly coastal slope with short patchy vegetation, 52 m, 29S 049282/438393, 2010.12.25, GAH and DTH – P91, 3 sh, CGAH; S. Bartolomeu, 2 km SE. of Nazaré, granitic hill with crags, wooded slopes and old buildings, 155 m, 29S 04955/43825, 2011.06.04, GAH and DTH – P162, 7 sh, CGAH; just SW. of Vale de Parades, narrow strip of dune vegetation at base of cliff slope, 12 m, 29S 049561/439426, 2010.12.25, GAH and DTH – P92, 4 sh, CGAH; Pedras Negras, ca 3 km N. of S. Pedro de Moel, dunes with patchy low grasses and herbs, 20 m, 29S 049813/440313, 2010.08.12, GAH and DTH – P68, 1 sh, not kept; Serra da Arrábida, N.- to NW.-facing limestone crags and rocky slopes, 380 m, 29S 05021/42601, 2007.05.17, GAH – 2007.10, 5 sh, CGAH, mixed with *O. barbula*; Serra da Arrábida, N.- and S.-facing rocky limestone slopes with patches of scrub, 388 m, 29S 05020/42602, 2011.02.12, GAH and DTH – P129, 8 (5) sp, 3 sh, CGAH, mixed with *O. barbula*; Serra da Arrábida, S.-facing limestone crags and rocky slope, 300-350 m, 29S 05032/42604, 2007.05.17, GAH – 2007.11, 15 sh, CGAH; Serra de Arrábida, high on rocky S.-facing limestone slope with patchy low scrub, 351 m, 29S 05032/42604, 2011.02.12, GAH and DTH – P128, 20 (3) sp, 10 sh, CGAH; Lisbonne, G. Servain, 1 sh, MHNG 17060, from river floodline debris; Minho: Ofir (SE. of Esposende), low sand dunes with patchy bushes, herbs and grassland, 9 m, 29T05175/45972, 2011.08.30, GAH and DTH – P190, 2 sh, not kept; Valença fortress, Valença, 29TNG2953, 2009.04.08, ÁDO, (2) sp, CGAH; Monção fortress, Monção, 29TNG4258, 2009.01.30, ÁDO, (3) sp, CGAH; N. edge of Peneda village, rocky granitic slope with old walls, patchy grasses and herbs, 688 m, 29T 056447/464734, 2011.08.29, GAH and DTH – P187, (1) sp, not kept; ca 2 km N. of Lamas de Mouro, rocky mountain slope, facing S., sparse low vegetation, 1080-1100 m, 29T 05665/46570, 2011.08.29, GAH and DTH, 1 sh, not kept, old shell only; Trás-os-Montes: Penas Róias Castle, Mogadouro, 29TPF9685, 2009.11.10, ÁDO, (1) sp, CGAH; by IP2/N103-7 ca 2 km NNE. of Rabal, beside irrigation channels in *Fraxinus* grove with few *Quercus*, 618 m, 29T 06873/46388, 2011.06.29, GAH – P170, 2 sh, not kept; Bragança castle and Fervença River, Bragança, 29TPG 8630-8730, 2009.11.11, ÁDO, (3) sp, CGAH; by N218 ca 4 km due NW. of Vimioso, slopes of river gorge with crags (slate and schist), screes and patchy scrub, 447 m, 29T 070334/460939, 2011.06.30, GAH and DTH – P171, 2 sh, not kept; ca 1 km S. of Vale de Águia (NE. of Miranda do Douro), exposed low and flat granitic rocks with boulders, patchy scrub and low evergreen *Quercus* trees, 672 m, 29T 0729638/4600096, 2011.07.01, DTH – P172, (3) sp, not kept; Spain, Prov. Cáceres: by EX117 at Rio Salor, NE. of Membrio, slopes of slaty rock above river banks with patchy low vegetation, 159 m, 29S 067198/438245, 2010.12.23, GAH and DTH – E89, (1) sp, 4 sh, CGAH; by EX302 at Rio Salor, NE. of Herreruella, slopes of slaty rock above river banks with patchy low herbs and scrub, 209 m, 29S 068226/437263, 2010.12.23, GAH and DTH – E90, (2) sp, 1 sh, CGAH; Prov. La Coruña: E. edge of P. N. de Corrubedo, exposures of low granite rocks with moss locally and very sparse grasses, at edge of *Pinus* wood, 48 m, 29T 049808/471162, 2011.08.27, GAH and DTH – E183, 1 sh, not kept; Prov. León: by N536 ca 1 km S. of Salas de la Ribera, low roadside cutting, crag and scree of slaty rock with sparse low grasses and herbs (bushes above), 393 m, 29T 06796/46993, 2011.10.16, GAH and DTH – E213, 5 sh, not kept; NW. of Almazcara, low banks between grassland and road, above shallow ditch, with patchy grasses and herbs, bushes locally, 672 m, 29T

07035/47203, 2011.10.16, GAH and DTH – E212, 3 sh, not kept; Prov. Ourense: by OU533 0.5 km S. of Santa Cruz, low granitic rocks of road cutting with short patchy herbs and grasses, bushes locally, 621 m, 29T 065415/468485, 2011.10.17, GAH and DTH – E214, 2 sh, not kept; *ca* 1 km W. of San Tirso (Sierra de la Encina), N.-facing crags and slopes of hard limestone, *ca* 870 m, 29T 06701/47089, 2007.05.21, GAH – 2007.19, 1 sh, CGAH; by OU533 near Cemiterio *ca* 2 km S. of Santa Cruz, granitic rocks and slopes by road, with sparse herbs and few bushes, 648 m, 29T 065406/468446, 2011.10.17, GAH and DTH – E215, 5 sh, not kept; Prov. Pontevedra: la Lanzada (S. of O Grove), sand dunes with low vegetation, 8 m, 29T 05107/46992, 2011.08.26, GAH and DTH – E180, 2 sh, not kept; *ca* 3 km NW. of Sanxenxo, top of slaty sea-cliffs with low scrub and patches of grasses and herbs, *ca* 15 m, 29T 051032/469590, 2011.08.26, GAH and DTH – E181, (3) sp, CGAH; just NW. of San Vincente do Grove, open slopes above beach with blown sand over granite, patchy herbs and grasses, 15 m, 29T 050522/470284, 2011.08.27, GAH and DTH – E182, (2) sp, not kept; Prov. Zamora: by N631 at E. N^o S^a de Argavanzal (S. of Rionegro del Puente), slopes above reservoir edge with outcrops of metamorphic rock, patchy grassland, bushes and saplings, 797 m, 29T 072914/465153, 2011.10.17, GAH and DTH – E216, 2 sh, not kept.

O. barbula, Portugal, Beira Baixa: by IC8 just NE. of Ansião, woodland and grassland on limestone, 210 m, 29S 054915/441926, 2011.04.29, GAH and DTH – P141, (2) sp, CGAH; Beira Litoral: Serra de Sico (summit area), rocky limestone slopes with patchy low scrub and grassland, 548 m, 29S 053909/441909, 2011.01.13, GAH – P98, (3) sp, 10 sh, CGAH; Pombal Castle, 29SNE3218, 2008.04.24, ÁDO, 6 (3) sp, CGAH; *ca* 0.5 km S. of IC8 at *ca* 1.5 km WNW. of Ansião, limestone slopes with scrub, crags and grassland, *ca* 194 m, 29S 05466/44185, 2010.09.26, GAH and DTH – P73d, (1) sp, 23 sh, CGAH; 0.5 km S. of IC8 at *ca* 2 km WNW. of Ansião, rocky limestone slopes with scrub above, *ca* 190 m, 29S 054642/441843, 2010.09.26, GAH and DTH – P75, 2 sh, not kept; Vale da Couda (SE. of Almoester), limestone valley with low crags and patchy *Quercus* woodland, *ca* 263 m, 29S 05487/44103, 2010.05.29, GAH and DTH – P45, (1) sp, CGAH; *ca* 1.5 km W. of Ansião, low *Quercus* woodland on slope with limestone rocks, *ca* 239 m, 29S 05466/44179, 2010.09.26, GAH and DTH – P74, 3 sh, not kept; *ca* 1 km SW. of Ateanha village (E. of Alvorge), S.-facing limestone hillside with grassland, patchy scrub and rocks, 310 m, 29S 05498/44262, 2010.05.29, GAH and DTH – P46, (1) sp, CGAH; S. of IC8 at *ca* 3 km W. of Avelar, limestone slopes with short grasses and herbs, scrub locally, 288 m, 29S 05520/44192, 2011.02.24, GAH and DTH – P133, 9 sh, CGAH; *ca* 1 km SW. of Alfarelos, limestone crags and grassland, 13 m, 29T 05283/44439, 2010.11.03, GAH and DTH – P79, (4) sp, 8 sh, CGAH; by Paul do Taipal near Montemor-o-Velho, disused limestone quarry with patches of short vegetation, 45 m, 29T 05271/44481, 2011.01.09, GAH – P96, (3) sp, 6 sh, CGAH; by Ruínas de Conimbriga, open *Olea* grove with grassland and herbs beneath, *ca* 100 m, 29T 054352/443878, 2010.04.27, GAH and DTH – P39, 1 sh, CGAH, old shell only; Conimbriga, Condeixa-a-Nova, 29TNE4339, 2008.10.26, ÁDO, (3) sp, CGAH; by Rio de Mouros, S. of Condeixa-a-Velha, deciduous woodland with rocky limestone banks beside stream, *ca* 117 m, 29T 05436/44386, 2010.04.27, GAH and DTH – P38, 2 sh, CGAH; Castelo do Rabaçal, rocky limestone slopes, grassland and scrub, *ca* 315 m, 29T 05489/44309, 2010.04.27, GAH and DTH – P40, 1 sh, CGAH; Penela Castle, 29TNE5231, 2008.10.13, ÁDO, (2) sp, CGAH; Estremadura: Serra da Arrábida, limestone crags and rocky slopes (S.-facing), 250 m, 29S 04999/42576, 2007.05.16 and 18, GAH – 2007.9 and 15, 68 sh, CGAH; Serra de Arrábida, rocky limestone slope and road cutting facing S. and E., with patchy scrub, 263 m, 29S 05000/42577, 2011.02.12, GAH and DTH – P130, 4 (3) sp, 9 sh, CGAH; Serra de Arrábida, herbs and grasses at base of S.-facing limestone road cutting, 131 m, 29S 050117/425874, 2011.02.12, GAH and DTH – P131, (1) sp, 12 sh, CGAH; Serra de Arrábida, N.- to NW.-facing limestone

crag and rocky slopes, 380 m, 29S 05021/42601, 2007.05.17, GAH – 2007.10, 12 sh, CGAH, mixed with *O. barbella*; Serra de Arrábida, N.- and S.-facing rocky limestone slopes with patches of scrub, 388 m, 29S 05020/42602, 2011.02.12, GAH and DTH – P129, 4 sp, 6 sh, CGAH, mixed with *O. barbella*; Serra de Montejunto, rocky limestone slopes and crags with low scrub and varied herbs, ca 400 m, 29S 04950/43382, 2010.04.19, GAH – P34, 2 sh, not kept; ca 2.3 km NE. of São Pedro de Moel, crevices amongst limestone boulders at base of wall of road bridge by stream, 35 m, 29S 049877/440268, 2010.08.12, GAH and DTH – P67, (3) sp, 12 sh, CGAH, atypical shells (see text); ca 2 km NNE. of São Pedro de Moel, bank 2 m above stream in *Eucalyptus* woodland on coastal sands, 20 m, 29S 049872/440265, 2011.06.04, GAH and DTH – P161, (4) sp, 4 sh, CGAH, atypical shells (see text); Fórnea (SE. of Alcaria), limestone crags, screes and slopes, patchy scrub, ca 275 m, 29S 05170/43789, 2010.05.02, GAH and DTH – P43, 10 sh, CGAH; ca 1 km SW. of Serro Ventoso, rocky limestone slopes and road cutting, scrub and wooded slopes, ca 380 m, 29S 05140/43784, 2010.07.19, GAH and DTH – P59, 13 sh, CGAH; Serro Ventoso, Porto de Mós, 29SND1479, 2008.02.12, ÁDO, 3 (2) sp, CGAH; ca 2 km NW. of Serro Ventoso, rocky limestone slope with low crags and scrub, 29S 05129/43809, 2010.07.30, GAH – P62, 9 sh, CGAH; valley 0.5 km E. of Livramento, limestone valley with patchy scrub and low rocks, 174 m, 29S 05168/43814, 2010.08.06, GAH and DTH – P65, 21 sh, CGAH; ca 1.5 km SE. of Livramento, rocky limestone slopes facing E. below crag, with evergreen *Quercus* woodland, 290 m, 29S 05170/43806, 2010.08.06, GAH and DTH – P64, 19 sh, CGAH; ca 0.5 km SE. of Livramento, rocky limestone slope with grassland and scrub, 238 m, 29S 05170/43809, 2011.03.22, GAH – P136, 2 sh, not kept; Ribatejo: SE. of Moitas Venda, limestone crags and rocky slopes with scrub, ca 195 m, 29S 05311/43717, 2010.05.02, GAH and DTH – P41, (2) sp, 27 sh, CGAH; Convento de Cristo, just W. of Tomar, convent and castle walls and ruins, old gardens, 126 m, 29S 05499/43839, 2011.08.05, GAH and DTH – P175, 6 sh, not kept; ca 2 km NNE. of Santa Cita, river banks with mature trees, dumped masonry, *Ulmus* grove, roadside verge and grassy banks, 65 m, 29S 05526/43795, 2011.08.05, GAH and DTH – P176, 9 (4) sp, CGAH; locality unknown: leg. Holl, 1 sh, SMF 7035, Paralectotype, 1 sh, SMF 7036, Lectotype.